REDESCRIPTION OF THE LARVA OF *GOMPHUS MILITARIS* HAGEN (ODONATA: GOMPHIDAE), WITH DISTRIBUTIONAL AND LIFE HISTORY NOTES

BRETT H. P. LANDWER AND ROBERT W. SITES

Enns Entomology Museum, Department of Entomology, and Center for Agroforestry, University of Missouri, Columbia, MO 65211, U.S.A. (e-mail: bhl065@mizzou.edu and SitesR@missouri.edu)

Abstract.—The final larval instar of Gomphus militaris Hagen is described, diagnosed, and figured from exuviae and larval specimens from Missouri, Texas, and Kansas. A previous description was erroneously attributed to G. militaris, but actually pertained to Arigomphus lentulus. Thus, the use of many previously published characteristics to identify this species will result in misidentification. Larvae of G. militaris were common and widespread in ponds in the prairie region of Missouri. We report data on life history based on larval and adult collections.

Key Words: Odonata, Gomphidae, Gomphus, Arigomphus, larva, Missouri

Gomphus militaris Hagen is primarily a species of the southern Great Plains of North America and has been reported from Iowa and North Dakota, south to New Mexico and Nuevo Leon, Mexico (Dunkle 2000, Needham et al. 2000). It was the "most frequent species of the genus" in Oklahoma (Bick and Bick 1957), the most widely distributed and commonly encountered species of Gomphidae in Texas (Abbott 2001), and common throughout Kansas (Huggins et al. 1976, Beckemeyer and Huggins 1997). Recently, it was reported to be common in western Missouri (L. Trial and J. F. Belshe, in litt.).

Due in part to its limited range, information regarding the ecology and life history of *G. militaris* is scant. It is a species of ponds or sluggish streams (Bird 1934; Beckemeyer and Huggins 1997; Dunkle 2000; L. Triał and J. E Belshe, in litt.) where the larvae burrow in the sediment and detritus along the margins (personal observation). The adult flight season is 19 March to 15 August in Texas (Abbott 2001), and June and July in Kansas (Beckemeyer and Huggins 1997). In Texas, most specimens collected between 18 May and 1 June were reported to be teneral (Bick and Bick 1957). In Oklahoma, the peak of larval emergence occurred during mid-May (Bird 1934). Specimens reared in Kansas by D. G. Huggins emerged during early June (unpublished data).

We conducted a survey of the larval Odonata of ponds in the prairie (*sensu* Steyermark 1963, Pfleiger 1989, Bailey 1998) or plains (*sensu* Branson 1944, Thornbury 1965, Thom and Wilson 1980, Omernick 1987) regions of Missouri in 1998 and 1999. When determining specimens collected during this survey, we repeatedly encountered a single morphospecies of Gomphidae that could not be determined using existing keys that include the Midwestern fauna (i.e., Needham and Westfall 1955, Needham et al. 2000). These larvae superficially resembled those of the genus Ari-

gomphus Needham in general form and most often keyed to that genus. However, these larvae lacked the large, jagged teeth on the labial palps and the mid-dorsal ridge characteristic of larvae of Arigomphus. Moreover, adults of G. militaris frequently had been collected at ponds in the region, but no larvae had been encountered that could be attributed to this species using the published characters. However, our larvae possessed several characteristics which were contradictory to those attributed to G. militaris in the existing keys (i.e., Needham and Westfall 1955, Young and Bayer 1979, Needham et al. 2000) and in the larval description given by Bird (1934).

Specimens were sent to K. J. Tennessen who determined that they were indeed *G. militaris* and informed us that larvae of this species may not agree with published characters (personal communication). We also reared a male specimen and determined it as *G. militaris*. We present a redescription of the larva of *G. militaris*, with distributional data and notes on its life history in Missouri.

MATERIALS AND METHODS

We measured 10 specimens: exuviae of one partially emerged male specimen, exuviae of one unreared final instar, and eight final instars. Three of the larvae were from Texas, one from Kansas, and the remaining six specimens from Missouri.

All measurements were performed in dorsal view and represent maximum values. unless otherwise stated. Due to non-uniform telescoping of the abdomen, exact measures of total length and length of abdomen are impossible to obtain (see Calvert 1934, Huggins and Harp 1985). Therefore, these measurements were performed to the nearest mm using calipers. All other measurements were performed using an ocular micrometer. The head was measured from the anterior margin of the clypeus to the posterior margin of the postocciput, and the abdomen to the tip of the caudal appendages. The outer surface was considered the dorsal aspect of the leg. Wingpads were

measured from the dorsal juncture with the thorax to the tip. Mid-dorsal and mid-ventral abdominal segment lengths were measured from anterior to posterior margins of a sclerite, excluding dorsal hook, if present. Lateral margins of abdominal segments were measured from the anterolateral corner to the tip of the lateral spine. Lateral spines were measured from the posterior margin of the tergite immediately adjacent to the spine, to the tip of the spine. Basal width of abdominal segments were maximum values, measured just beyond the slight basal constriction. To compensate for lateral distortion of the abdomen in exuviae and preserved larvae (see Tennessen and Louten 1984, Huggins and Harp 1985), the abdomen was depressed for abdominal segment width measurements (except segment X) so that the ventral surface was flat in cross section. Caudal appendages were measured from the posterodorsal margin of segment X to the tip of the appendage.

SYSTEMATICS

Gomphus militaris Hagen

Description.—Total length 28–30 mm (mode = 30 mm). Overall body shape clongate fusiform, slightly depressed (Fig. 1). Body color light brown with darker brown markings. Dorsal surface of body finely granulose with glabrous patches on muscle scars. Minute, scalelike setae emanating from granules. Ventral surface generally not granulose, but with very fine setae. Larvae collected *in situ* with fine dorsal setation generally obscured by layer of fine silt and detritus.

Head: Width 5.25–5.67 mm ($\bar{y} = 5.50$), length 3.08–3.33 mm ($\bar{y} = 3.21$). Posterolateral margins abruptly rounded. Clypeus extending anteriorly to apex of second antennal segment, labrum to about middle of third segment. Compound eyes with mesal margins converging posteriorly. Antenna with segments III and IV darker than light brown general body color, segment III expanding slightly to apex and bowed up-



Figs. 1–4. Gomphus militaris larva. 1, Dorsal view of larva. 2, Ventral view of labian 3, Blade of labial palp (detail of inset of Fig. 2). 4, Dorsal view of abdominal segments VII–X and terminal appendages of female.

ward. Ratio of antennal segment lengths 5: 3:13:1. Prementum, in ventral aspect, constricted in proximal ca. ¹/₃, lateral margins subparallel in apical ²/₃ (Fig. 2). Mid-ventral length of prementum, excluding hinge, 3.20-3.32 mm ($\bar{y} = 3.25$), width 2.40-2.64mm ($\bar{y} = 2.51$). Anterior margin of prementum between bases of labial palps (ligula) evenly convex with dense fringe of long, stout, scalelike setae, and without distinct median tooth (Fig. 2). Blade (first segment) of labial palp rounded apically, with $7-12 \pmod{9}$ very short, nearly obsolete, squarely truncate teeth along the slightly arcuate mesal margin, distal-most tooth triangular but not longer than remaining teeth (Fig. 3). Long, conspicuous hairs on antennal segments, distal margin of labrum, and lateral margin of head beneath the compound eye from base of antennae to postocciput. Glabrous areas on dorsum of head comprising proximal portion of clypeus; V-shaped spot in center of frons; oval area lateral to V-shaped spot and adjacent to mesal margin of compound eye; spots immediately anterior to postocciput at midline and ca. 3/2 length from mid-line to posterolateral corner; thin, elongate spot above posterolateral corner.

Thorax: Areas of darker pigmentation variously developed, comprising margins of mesothoracic spiracle; dorsal portion of meso- and metapleural sutures; thin, longitudinal line dorsally between mesepisterna; immediately lateral to anal angle of metathoracic wingpads. Prothorax with ring shaped glabrous area lateral to mid-line, confluent anterolaterally with glabrous area on pleuron above base of coxa. Glabrous areas also present on and immediately adjacent to meso- and metapleural sutures. Fringe of long, conspicuous hairs along lateral margins of thorax. Pigmentation of legs slightly darker at apex of tibia. Legs hairy, with distinct fringes on dorsal and ventral surfaces. Pro- and mesotibial borrowing hooks well developed. Length of hind femur 5.42–5.83 mm ($\bar{y} = 5.53$ mm), apex attaining ca. mid-length of abdominal segment IV. Glabrous areas of legs comprising triangular areas on both anterior and posterior surfaces of coxae; triangular area on the ventral surface of trochanters; longitudinal lines extending from base to near apex of femora on anterior, posterior, and dorsal surfaces; similar, less conspicuous lines on tibiae. Length of metathoracic wingpad 6.42–6.83 mm ($\bar{y} = 6.61$ mm), attaining ca. mid-length of abdominal segment IV. Mesothoracic wingpad slightly overhanging anterior margin of abdominal segment IV. Wingpads densely granulose and pubescent on margins, less so on major veins of metathoracic wingpads, remainder glabrous. Dark coloration at nodi and tips of mesoand metathoracic wingpads, and proximal anal region of metathoracic wingpad.

Abdomen: Slender and gradually tapering to tip (Fig. 1), moderately depressed. Lateral margins with fringe of long setae. Posterior margin of tergites with sparse fringe of shorter setae, densest near midline. Length of abdomen 18-21 mm (mode = 21 mm), maximum width 7.0–7.4 mm (\bar{y} = 7.2 mm). Integument glabrous at muscle scars, external surfaces of terminal appendages, and entirety of segment X. Segments I-VIII dorsally with paired dark spots near mid-length of each segment just lateral to mid-line (Fig. 4). Mesal margin of each muscle scar also with dark spot. Segment IX with dark spot at posteromedial corner of muscle scar (Fig. 4). Spots absent from segment X, and fading on segments anterior to IV. Lateral margins diverging moderately to segment IV, converging gradually beyond segment V to parallel-sided segment X (Fig. 1). Dorsal mid-line without ridge or impressed line. Segments I-VII with low, posteromedial protuberance occupying ca. 1/2 length of segment. Posteromedial protuberance of segment VIII very low. Female with rudimentary lobes of vulvar lamina projecting slightly from posterior margin of abdominal sternite VIII. Dorsum of segment IX, in cross section, nearly tectate anteriorly, circular posteriorly. Mid-dorsal length of segment IX, excluding hook, 8399% ($\bar{v} = 92\%$) basal width, and 84–94% $(\bar{y} = 87\%)$ mid-ventral length. Segment 10 cylindrical. Basal width of segment X 83-97% ($\bar{v} = 93\%$) mid-dorsal length. Lateral spines present on abdominal segments VII-IX (rarely a minute spine on VI). Lateral spines of VII and VIII small, comprising 8-14% ($\bar{y} = 10\%$) and 11-20% ($\bar{y} =$ 13%), respectively, of lateral margin of segment. Lateral spine of segment 1X long, slender, and somewhat appressed to side of segment X, 36–50% ($\bar{v} = 43\%$) as long as mid-dorsal length of segment X, usually extending slightly short of mid-length of segment X. Length of lateral spine of segment IX 0.56–0.72 mm ($\bar{v} = 0.64$ mm). Mid-dorsal posterior hook present on segment IX, usually present on segment VIII, and occasionally present on segment VII. Hook on segment VIII and VII, if present, minute and formed by gradual recurvature of posterior margin of tergite on either side immediately lateral to mid-line, to form an acuminate process. Hook of segment 1X flat, slightly larger than that of segment VIII, more abruptly protruding from posterior margin of tergite, and slightly overhanging anterior margin of segment X. Length of epiproct 80–88% ($\bar{y} = 84\%$) middorsal length of abdominal segment X, and 93–100% ($\bar{y} = 97\%$) length of paraprocts. Male epiproct, in dorsal view, abruptly narrowed immediately beyond mid-length, forming a pair of rounded, lateral humps. Female epiproct tapering more regularly to tip (Fig. 4). Length of cercus 83–96% ($\bar{y} =$ 92%) that of epiproct.

Diagnosis.—The larva of *Gomphus militaris* can be distinguished from North American congeners by the following combination of characters: length of abdominal segment X subequal to or decidedly greater than basal width; mid-dorsal length of abdominal segment IX subequal to or less than basal width; lateral spines of abdominal segment V1 absent or minute; distal margin of labial palp rounded and without end hook; teeth of labial palp truncate and nearly obsolete. *Gomphus militaris* can be distinguished from species of Arigomphus by the absence of a mid-dorsal ridge on the anterior portion of the middle abdominal tergites, and the teeth of the labial palp small, squarely truncate, and much shorter than basal width. Examination of earlier instar specimens indicates that these characteristics are quite stable in specimens as small as ca. 15 nm in total length. Abdominal segment X becomes slightly more clongate and the lateral spines of IX extend a proportionately shorter distance in progressively earlier instars.

Material examined.-TEXAS: Kimble Co.; N. Llano R. 1.7 mi. W. on Rt. 377, V-24-1987, RWS, 1 larva; Mason Co.: James R. near London, IV-11-1992, RWS, 2 larvae: KANSAS: Elk Co.: Big Caney R.-1 mi. W. Grenoda at U.S. 160 hwy. br., V-12-1982, B. Coler & D. G. Huggins, 1 larva: MISSOURI: Audrain Co.: Robert M. White II Conservation Area, UTM (Universal Transverse Mercator) zone 15 597050E, 4353000N, IV-24-1999, BHPL & N. Whiteman, 1 larva; Boone Co.: Ashland Lake, UTM zone 15 568980E 4290420N, V-6-2001, BHPL, 1 male (partially emerged V-26 2001); Caldwell Co.: Bonanza Conservation Area, UTM zone 15 418010E 4385720N, 111-10-1999, BHPL & N. Whiteman, I larva; Monroe Co.: Otter Cr., UTM zone 15 569650E 4384400N, VI-21-2001, BHPL, exuviae (1 specimen); Platte Co.: Guy B. Park Conservation Area, UTM zone 15 345150E 4365040N, 111-21-1999. BHPL & N. Whiteman, 1 larva; Vernon Co.: Douglas Branch Conservation Area, UTM zone 15 379030E 4198180N, III-22-1999, BHPL & N. Whiteman, 1 larva.

Additional Missouri material examined.—Atchison Co.: Tarkio Prairie Conservation Area, BHPL & N. Whiteman, UTM zone 15 313200E 4485890N, IX-12– 1998; same data, UTM zone 15 312230E 4486100N, BHPL & N. Whiteman; Audrain Co.: Robert M. White II Conservation Area, UTM zone 15 597100E 4353150N, IX-9-1998, BHPL & N. Whiteman; Barton Co.: Shawnee Trail Conser-

vation Area, UTM zone 15 359735E 4143150N, 1X-26-1998; Dorris Creek Prairie Conservation Area, UTM zone 15 390765E 4137060N, IX-27-1998, BHPL & N. Whiteman; same data, VI-9-1999, BHPL & N. Whiteman; Clear Creek Conservation Area, UTM zone 15 390900E 4166300N, VI-9-1999, BHPL & N. Whiteman; Carroll Co.: Bunch Hollow Conservation Area, UTM zone 15 449350E 3380150N, 1X-13-1998, BHPL & N. Whiteman; Harrison Co.: Wayne Helton Memorial Conservation Area, UTM zone 15 432000E 4454000N. VI-23-1999, BHPL & N. Whiteman; Henry Co.: Connor O. Fewel Conservation Area, UTM zone 15 439600E 4259650N, IX-20-1998. BHPL & N. Whiteman: Holt Co.: Riverbreaks Conservation Area, UTM zone 15 321210E 4420700N, VI-15-1999, BHPL & N. Whiteman: Knox Co.: Henry Sever Lake Conservation Area, UTM zone 15 587200E 4429840N, 1X-6-1998, BHPL & N. Whiteman; Lafavette Co.: Maple Leaf Lake Conservation Area, UTM zone 15 431410E 4316450N, IX-18-1998, BHPL & N. Whiteman; Livingston Co.: Poosey Conservation Area, UTM zone 15 442000E 4420220N, 1X-12-1998, BHPL & N. Whiteman: St. Clair Co.: Taberville Prairie Conservation Area, UTM zone 15 414800E 4211890N, IX-26-1998, BHPL & N. Whiteman; Vernon Co.: Little Osage Prairie Natural Area, UTM zone 15 381800E 4180440N, IX-26-1998, BHPL & N. Whiteman; Worth Co.: Emmett and Leah Seat Memorial Conservation Area, UTM zone 15 396450E 4471620N, 1X-12-1998, BHPL & N. Whiteman.

DISCUSSION

The results demonstrate that previously published characters will not correctly distinguish larvae of *Gomphus militaris* from those of congeners. In their key to species of the subgenus *Gomphus*, Needham and Westfall (1955) characterized *G. militaris* as the only species of the subgenus not possessing lateral spines on abdominal segments VII and VIII. As such, the larva of *G. militaris* will key to *G. spicatus* Hagen with Needham and Westfall (1955). This shortcoming is corrected only partially by Needham et al. (2000), who characterized *G. militaris* as possessing lateral spines on abdominal segments VIII and IX, or IX only. In that key, the larva can not be keyed to any species. As shown here, lateral spines are present on abdominal segments VII–IX.

The results of this analysis also reveal the inadequacy of existing keys to reliably distinguish G. militaris from species of Arigomphus. The abdomen of species of Arigomphus has been characterized as tapering, whereas that of species of Gomphus as ending more abruptly (Needham and Westfall 1955, Young and Bayer 1979, Needham et al. 2000). However, the abdomen of G. militaris is tapering, as in species of Arigomphus. Also, abdominal segment X of species of Arigomphus has been characterized as "distinctly" longer than wide (Young and Bayer 1979, Needham et al. 2000) and segment IX as wider than long (Needham et al. 2000), whereas abdominal segment X in species of Gomphus has been characterized as not longer than wide (Young and Bayer 1979), or if longer, then with segment IX longer than wide (Needham et al. 2000). As shown here, segment X of G. militaris is usually longer than wide, but abdominal segment IX is not. Finally, species of Gomphus with the abdomen acuminate and abdominal segment X longer than wide have been characterized as possessing large end hooks on the labial palps (Needham et al. 2000); however, G. militaris possesses no such end hooks.

The inability of published characters to diagnose the larva of *G. militaris* is not due to intraspecific variation. Larvae from throughout the range of this species were consistent in the manifestation of key characteristics. In addition to the specimens measured in the description, six final instar exuviae, reared by D. G. Huggins, and numerous larvae from Kansas (Kansas State Biological Survey collection, housed at the University of Kansas Natural History Museum and the Snow Museum of Entomology) were examined but not measured, and diagnostic characters were consistent throughout. Further, although Young and Bayer (1979) accurately figured the labium and abdomen of *G. militaris*, the characters provided in their key were inadequate to diagnose the species.

Much of the confusion can be traced to the published larval description by Bird (1934), upon which existing keys seem, at least partially, to be based. Bird's description was based on the exuviae from the emergence of a single female from a pond in Oklahoma on V-10-1932. The teneral imago escaped "one hour and seventeen minutes after the nymph had left the water." The association was based upon photographs and notes of the teneral imago. The senior author has examined the exuvial specimen described by Bird and determined it to be that of *Arigomphus lentulus* (Needham).

Determination of female specimens of Gomphidae is difficult, even when working with mature material in the laboratory, and field identification of teneral specimens is highly suspect. Additionally, adult specimens of *Arigomphus* are less darkly pigmented than those of related genera, and *G. militaris* displays reduced dark markings relative to other species of the genus *Gomphus*. Further, the nymph of *A. lentulus* was unknown at the time of Bird's description. Thus, Bird's field identification was a reasonable error.

The description by Bird was the first formal description of the larva of *A. lentulus*, and should be cited as such. There can be little doubt that the exuviae examined by BHPL are those described by Bird. The vial bears his determination label as *Gomphus militaris*, and the female specimen was collected by Bird in McClain Co., Oklahoma on V-10-1932, which matches the data given in his description. Only one specimen bearing this information was found in Bird's collection, housed at the Sam Noble Oklahoma Museum of Natural History, University of Oklahoma (Ken Hobson, personal communication). No information regarding an associated imago is recorded on the label. The specimen exactly matches Bird's figures and agrees with the description, except on two points: Bird stated that lateral spines are present only on abdominal segment IX, and that no dorsal "teeth" are present on any abdominal segment. However, the figures which accompany Bird's description clearly depict a small dorsal hook on abdominal segment IX, and indicate lateral spines on at least segments VIII and IX. The specimen does, in fact, bear a small dorsal hook on segment IX, and small lateral spines on segments VII and VIII in addition to the large lateral spines of segment IX. Additionally, it should be noted that other larval specimens of A. lentulus often bear a small dorsal hook on segment VIII. Interestingly, as evidenced by Bird's description, the length of abdominal segment X of specimens of A. lentulus often is no greater than the basal width.

Gomphus militaris was the most frequently encountered species of the family Gomphidae in ponds in the prairie region of Missouri. Final instars were collected only during the spring, but much smaller instars were also collected at this time. Samples from early summer contained only intermediate instars, and samples from late summer contained both early and late instars. A final instar collected on 6 May died while emerging on 26 May, and exuviae were collected on 21 June. This emergence, coupled with adult collection data, establishes the flight season as 26 May to 5 August in Missouri. The instar distribution and flight season data indicate that G. militaris emerges somewhat synchronously during the spring and at least some individuals may require more than one year to complete development in Missouri.

The larval distribution records indicate that *G. militaris* is more widespread in Missouri than previously shown. The collection records from Shelby, Audrain, and Knox counties extend the known eastern limit of the species range ca. 150 km beyond that given in the most recently published, detailed account (Dunkle 2000). Also, the collection of exuviae from Shelby County demonstrates adult recruitment at this limit, and the Knox County record places the known limit within ca. 40 km of the Mississippi River.

ACKNOWLEDGMENTS

We thank Ken J. Tennessen for determination of specimens and a critical review of the manuscript. We are grateful to Jordan Yochim, University of Kansas Natural History Museum, and Dr. James S. Ashe, Snow Entomological Museum, University of Kansas, for the opportunity to examine material housed in their collections. Dr. Ken Hobson, Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, was instrumental in obtaining Dr. Bird's specimen. Linden Trial, Missouri Department of Conservation, provided adult material. Funding for RWS was provided in part by project #PSSL0232 of the Missouri Agricultural Experiment Station.

LITERATURE CITED

- Abbott, J. C. 2001. Distribution of dragonflies and damselflies (Odonata) in Texas. Transactions of the American Entomological Society 127: 189– 228.
- Bailey, R. G. 1998. Ecoregions—The Ecosystem Geography of the Oceans and Continents. Springer-Verlag, New York, 176 pp.
- Beckemeyer, R. J. and D. G. Huggins. 1997. Checklist of Kansas dragonflies. The Kansas School Naturalist 43: 1–16.
- Bick, G. H. and J. C. Bick. 1957. The Odonata of Oklahoma. The Southwestern Naturalist 2: 1–18.
- Bird, R. D. 1934. The emergence and nymph of Gomphus militaris (Odonata, Gomphinae). Entomological News 45: 44–46.

- Calvert, P. P. 1934. The rates of growth, larval development and seasonal distribution of dragonflies of the genus *Anax* (Odonata: Aeshnidae). Proceedings of the American Philosophical Society 73: 1– 70.
- Dunkle, S. W. 2000. Dragonflies Through Binoculars: A Field Guide to Dragonflies of North America. Oxford University Press, Oxford, 266 pp.
- Huggins, D. G. and G. L. Harp. 1985. The nymph of Gomphus (Gomphurus) ozarkensis Westfall (Odonata: Gomphidae). Journal of the Kansas Entomological Society 58: 655–661.
- Huggins, D. G., P. M. Liechti, and D. W. Roubik. 1976. Species accounts for certain aquatic macroinvertebrates from Kansas (Odonata, Hemiptera, Coleoptera, and Sphaeriidae), pp. 13–77. *In New Re*cords of the Fauna and Flora of Kansas for 1975. Technical Publications of the State Biological Survey of Kansas, no. 1.
- Needham, J. G. and M. J. Westfall, Jr. 1955. A Manual of the Dragonflies of North America (Anisoptera). University of California Press, Berkeley, 615 pp.
- Needham, J. G., M. J. Westfall, Jr., and M. L. May. 2000. Dragonflies of North America. Scientific Publishers, Gainesville, 939 pp.
- Omernik, J. M. 1987. Ecoregions of the conterminous United States. Annals of the Association of American Geographers 77: 118–125.
- Pflieger, W. L. 1989. Aquatic Community Classification System for Missouri. Aquatic series no. 19. Missouri Department of Conservation, Jefferson City, Missouri, 69 pp.
- Steyermark, J. A. 1963. Flora of Missouri. Iowa State University Press, Ames, 1,725 pp.
- Tennessen, K. J. and J. A. Louten. 1984. The true nymph of *Gomphus (Gomphurus) crassus* Hagen (Odonata: Gomphidae), with notes on adults. Proceedings of the Entomological Society of Washington 86: 223–227.
- Thom, R. H. and J. H. Wilson. 1980. The natural divisions of Missouri. Transactions of the Missouri Academy of Sciences 14: 9–23.
- Thornbury, W. D. 1965. Regional Geomorphology of the United States. John Wiley and Sons, New York, 609 pp.
- Young, W. C. and C. W. Bayer. 1979. The dragonfly nymphs (Odonata: Anisoptera) of the Guadalupe River Basin, Texas. The Texas Journal of Science 31: 85–97.